

Prey Capture by the Sea Anemone *Metridium senile* (L.): Effects of Body Size, Flow Regime, and Upstream Neighbors

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Abstract. The sea anemone *Metridium senile* is a quantitatively important passive suspension feeder in hard-bottom communities on the west coast of Sweden and occurs in aggregations with different size distributions. This study tests the hypothesis that different polyp sizes have different optimal flow regimes maximizing prey capture. Results showed that prey capture by *M. senile* is a function of both flow regime and polyp size, and different optimal flow regimes exist for different size classes. Large anemones had a maximum feeding efficiency at the slowest flow, medium-sized anemones at moderate flow, and small anemones at moderate- to high-flow regimes. Small anemones showed consistently higher feeding rates (per unit of biomass and area of tentacle crown) at all velocities above 10 cm s⁻¹ and exhibited less flow-induced deformation of the tentacle crown, suggesting that small anemones are better at feeding in moderate- to high-flow habitats. Different vertical projections of large and small anemones in the boundary layer could only partly account for differences in feeding success among size classes. Feeding rate was also a function of upstream conspecifics, declining asymptotically to 30% of the maximum rate. The negative effects of neighbors on feeding in aggregations with clonal rather than polyp growth appear to be compensated for by the generally higher feeding efficiency of small polyps.

Introduction

Flow habitat and body size are both important factors in the feeding biology of benthic, passive suspension feeders.

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Due to the nature of near-bottom hydrodynamics, however, flow exposure and body size are inseparable factors (Koehl, 1977a; Vogel, 1981). As suspension feeders grow taller they become exposed to faster currents within and beyond the substratum-associated boundary layer, and consequently to both greater drag and higher flux of potential prey (Wainwright and Koehl, 1976; Vogel, 1981). The height of a passive suspension feeder in a given flow habitat is therefore likely to involve a trade-off between maximizing food availability and minimizing flow forces and physical stress. In soft-bodied passive suspension feeders such as sea anemones, limitations as to how tall an individual can grow in a high-flow environment may, in part, be governed by the extent to which flow forces cause deformation of the feeding apparatus (Koehl, 1976, 1977a), reducing prey capture and thus energy for growth and reproduction (Sebens, 1979, 1981, 1982; Lesser *et al.*, 1994). Vertically oriented passive suspension feeders of different sizes are therefore likely to have different ranges of optimal flow velocities at which the physical stress is minimized and potential for prey capture is maximized. Many sessile cnidarians are, however, capable of polyp degrowth and indeterminate growth of the genet, in part through variable extents of asexual proliferation such as pedal laceration (Bucklin, 1987; Anthony and Svane, 1995), polyp fission (Francis, 1979; Sebens, 1980), and colony fission (McFadden, 1986). These capabilities result in size plasticity of the polyp (or colony) as well as of the clone. Small clones of large polyps (or colonies) in low-flow habitats and large clones of small polyps (or colonies) in high-flow habitats constitute alternative solutions for maximizing prey capture and the positive energy balance of the genet. In the latter case, however, the extent to which the relationship between polyp size, flow, and prey capture is modified by the presence of neighbor-

ing conspecifics (or clone members produced by asexual reproduction) has been demonstrated in only a few passive (octocorals: McFadden, 1986) and active (phoronids: Johnson, 1990; bryozoans: Okamura, 1992) suspension feeders.

In this paper, the sea anemone *Metridium senile* is used for testing the effects of flow, polyp size, and upstream neighbors on the feeding success of soft-bodied, passive suspension feeders. Five features render *M. senile* a good model for such studies: (1) The projected area of the tentacle crown increases more-or-less isometrically with body size (Sebens, 1981); (2) new tentacles of a determined size are added to the tentacle crown as the anemone grows (Sebens, 1979), so that the spacing and size of filtering elements are the same for large and small anemones; (3) the size of prey (zooplankton) taken does not increase significantly with anemone size (Purcell, 1977; Sebens, 1981; Sebens and Koehl, 1984); (4) it is capable of polyp degrowth (in part through asexual reproduction by pedal laceration) and thus has an intrinsic potential for adjusting its body size to the flow environment; and finally (5) it often forms dense, clonal aggregations (Anthony and Svane, 1994) in which prey capture per polyp is likely to be influenced by the presence of adjacent clonemates.

Metridium senile is a ubiquitous member of the hard-bottom community of most northern waters (Hoffmann, 1976; Fautin *et al.*, 1989) and occurs in different size distributions in different flow environments (Hoffmann, 1976, 1986; Shick *et al.*, 1979; Shick and Hoffmann, 1980; Anthony and Svane, 1994). For example, in high-flow channels on the west coast of Sweden where the current velocity frequently exceeds 100 cm s^{-1} , the walls and bottoms are carpeted by dense populations of small (2–3-cm-high) *M. senile*. Conversely, in low-flow habitats where the current rarely exceeds 5 cm s^{-1} , large (20–30-cm-high) *M. senile* predominate (Anthony and Svane, 1994, 1995). In moderate-flow habitats, populations of *M. senile* are generally composed of intermediate-sized anemones (Shick, 1991; and pers. obs.). Previous studies have suggested that differences in size distributions of *M. senile* can be attributed to the physical effects of flow on the anemone body plan (Koehl, 1977a; Shick and Hoffmann, 1980); genetic differences between local populations or clones (Shick *et al.*, 1979; Shick and Dowse, 1985; Hoffmann, 1986; Anthony and Svane, 1994); and effects of substratum instability, which influence the rate of laceration and thereby inversely affect polyp and clone size (Anthony and Svane, 1995). Trade-offs between polyp size and prey capture in different flow regimes are likely to structure populations of this ecologically and morphologically plastic species (Shick, 1991). Nevertheless, no studies have experimentally tested the hypothesis that different polyp sizes of *M. senile* have

different optimal flow regimes that reflect the size distributions in natural populations.

The objectives of this study are to (1) quantify prey capture in *M. senile* at a range of polyp sizes and flow velocities, (2) test whether combinations of polyp size and flow regime that maximize prey capture reflect size-frequency distributions found in different flow habitats *in situ*, and (3) test whether prey capture in *M. senile* is, in part, a function of the number of upstream conspecifics.

Materials and Methods

All experiments were conducted in a laboratory flume (300-cm long, 47-cm wide, 18–20-cm water depth), designed as described by Vogel (1981). A constant flow was ensured by controlling revolutions of the propeller by a Panasonic 501 inverter. Flow straighteners were mounted at the entrance of the flume channel to reduce turbulence to a level resembling near-bed field conditions. Prey used in all experiments were newly hatched nauplii of *Artemia salina*, which measure about $600 \mu\text{m}$ in length and are within the mid-range of prey sizes reported to be taken by *M. senile* in the field (Sebens and Koehl, 1984). *Artemia* nauplii do not show the escape responses characteristic of some natural prey (Trager *et al.*, 1994), so their use may produce overestimates of prey-capture rates *in situ*. That potential drawback was outweighed by the advantages that the non-evasive *Artemia* nauplii are less likely to confound flow effects on capture rates and can be reared in replicable batches.

Flow measurements

Feeding experiments were carried out at six preset flow regimes: 4, 10, 17, 20, 28, and 44 cm s^{-1} , measured at 10 cm above the flume floor by visually tracking and timing particles over a 25-cm trajectory within the working section of the flume. To determine the local flow velocity experienced by each anemone size class in a given flow regime, the vertical flow profile between 0.2 and 15 cm above the flume floor (1-cm intervals) was determined from a matrix of 16×6 point samples taken within a plane normal to flow. These local flow velocities were measured with a thermistor probe (LaBarbera and Vogel, 1976) calibrated according to the method described by Vogel (1981, p. 316). The development of a turbulent boundary layer was evident at all flow regimes, and the local flow velocities measured at 0.2–1 cm above the flume floor were generally 50% of those measured at a height of 10 cm (U_{10}). The flow profiles obtained in the flume at the six experimental flow regimes are depicted in Figure 1.

Distribution of nauplii in the flume

A comparison of the prey-capture success of different size classes of passive suspension feeders requires the as-

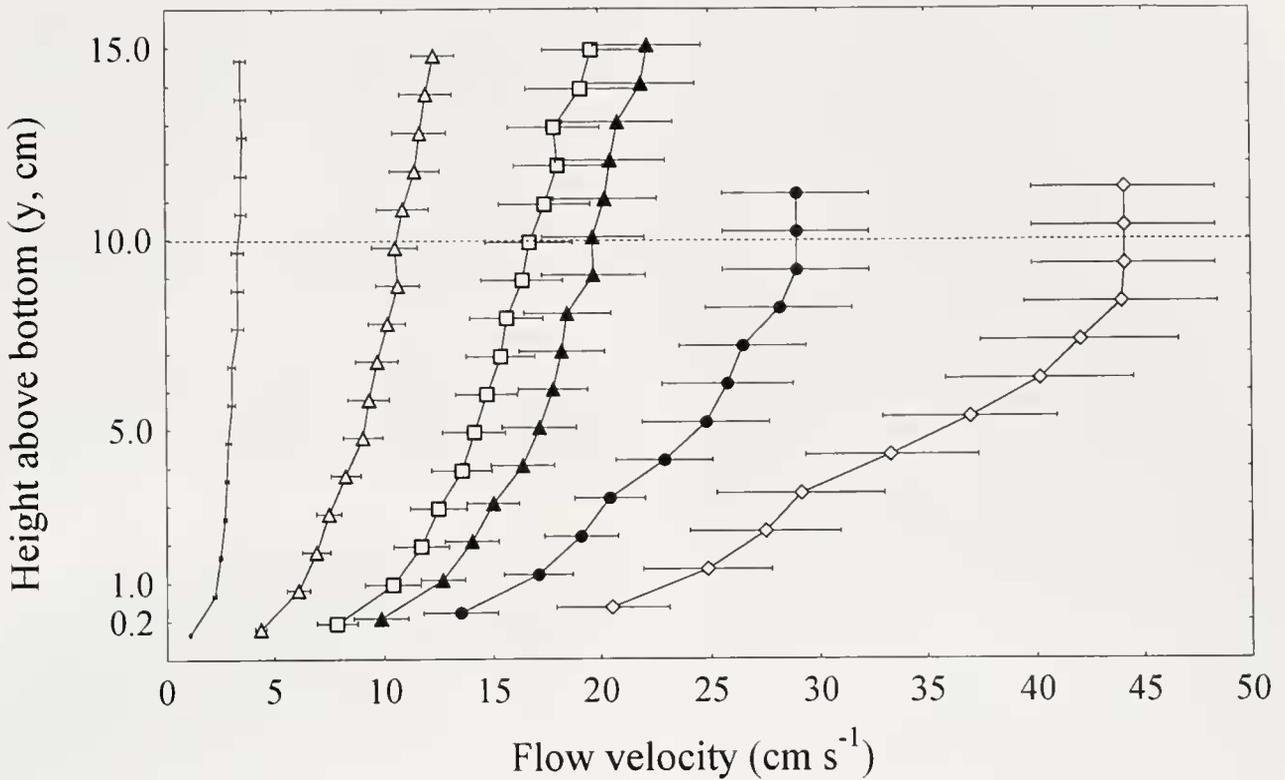


Figure 1. Flow profile as a function of flow regime in the working section of the flume. Flow regime is referred to as the velocity measured at 10 cm above the flume floor (U_{10}). Error bars represent ± 1 SE of 6 isobath measurements.

sumption of a uniform and constant distribution of prey items in the water column. Therefore, deviations from an even, vertical distribution of *Artemia* due to nauplii swimming or hydrodynamic sorting were determined by simultaneous sampling from 10 different heights above the bottom in the working section of the flume. Samples were collected with a comb of 4-mm acrylic pipes spaced 15 mm apart and pointing into the current, each pipe connected to a silicone tube (see Muschenheim, 1987). One-liter samples were taken at each height, and sampling was replicated three times (1-h intervals) for every flow regime. The numbers of nauplii were standardized to a percentage distribution and tested using a replicated *G*-test for goodness-of-fit (Sokal and Rohlf, 1981). Significantly higher concentrations of nauplii were found close to the bottom of the flume channel at $U_{10} = 4 \text{ cm s}^{-1}$ ($G_p = 55.4$, $P < 0.0001$) and $U_{10} = 10 \text{ cm s}^{-1}$ ($G_p = 20.1$, $P < 0.01$), but the vertical distribution was uniform at $U_{10} = 17, 20, 28$, and 44 cm s^{-1} ($P > 0.05$).

Vertical feeding zone and tentacle-crown deformation

The height range of the tentacle crown above the flume floor (measured at the uppermost (y_L) and lowermost

(y_B) tentacle tips) was determined for each group of anemones during experiments. These values were used to compare vertical feeding zones and local flow velocities experienced by different size classes and to calculate feeding efficiencies. Furthermore, the ratio of tentacle-crown surface area (S) to ash-free dry weight of individual polyps (AFDW) was used to indicate and compare the degree of tentacle-crown deformation caused by flow forces. Ash-free dry weight was used as denominator rather than a linear dimension because it provides the least variable measure of size. During each feeding experiment, tentacle-crown diameter (TCD, mean of two diameters taken at right angles to each other and described by the outermost tentacle tips) for each anemone was measured with callipers and used in calculating tentacle-crown area ($S = \pi(\text{TCD}/2)^2$).

Feeding experiments: sampling and experimental design

Three size classes of anemones within the full size range of *M. senile* were sampled in the Gullmarsfjord on the west coast of Sweden, from three sites that experience different prevailing current regimes. Large anemones

(6.0–6.5-cm pedal disc diameter, pdd) were collected in the central Gullmarsfjord where the current is generally low ($<5 \text{ cm s}^{-1}$), medium-sized anemones (2.5–3.0-cm pdd) were collected in a sound experiencing an intermediate current regime ($10\text{--}15 \text{ cm s}^{-1}$), and small anemones (1–2 cm pdd) were sampled in a narrow channel where the current frequently exceeds 100 cm s^{-1} (see also Anthony and Svane, 1994). In the laboratory, the anemones were allowed to attach to panels (terracotta tiles measuring 10 by 20 cm, 3 mm thick) submerged in seawater tables. Excess anemones were removed from the panels so that a single row of 2–4 contiguous anemones was established on each panel.

Prior to each experiment the flume was filled with filtered ($<20 \mu\text{m}$) seawater freshly collected at 30-m depth in the fjord (31–33‰ salinity and $8\text{--}11^\circ\text{C}$). The volume of the system when full (20-cm depth) was $400 \pm 2 \text{ l}$. Two panels with anemones attached were placed aligned on the bottom of the flume in the working section, so that a single row of 3–8 anemones was oriented perpendicular to flow. The anemones were allowed 12–24 h to acclimate to the selected flow regime and to fully expand before the feeding experiment was run. Immediately before an experiment, a standardized initial concentration (C_0) of $150 \pm 20 \text{ Artemia nauplii l}^{-1}$ was obtained by carrying out dilution series in 2000-ml beakers and calculating batch concentrations and C_0 . This concentration was assumed to be below that causing saturation of the anemones, since only a small percentage ($<5\%$) of the tentacles were occupied in prey capture at any given time. The overall prey capture obtained in the experiments was therefore assumed to be insignificantly affected by the C_0 chosen.

So that concentration of prey could be plotted as a function of time, five 140-ml water samples were taken simultaneously from the upstream section of the tank at $t = 0$ and after every 10 min during the following 70–90 min. Because the total sampling volume was less than 3% of the system volume, sampling volume was not replaced or corrected for in the analysis. Samples were taken using a rack of fixed pipettes (2 mm thick and 20 cm long) arranged along a horizontal transect normal to the direction of flow and connected by silicone tubes to a rack of syringes on the outside of the tank. Sampling was done manually and isokinetically during $30 \pm 3 \text{ s}$ to minimize variation due to prey patchiness. The samples were immediately filtered through a plankton mesh (60- μm) to give 50-ml concentrated suspensions, and the nauplii in each sample were counted directly using a dissecting microscope. The proportion of nauplii damaged by handling and by the flume propeller was less than 5%. To determine feeding relative to anemone biomass, the anemones were dislodged from the panels 24 h after each experiment, any food boluses were removed with a sy-

ringe, and anemones were frozen and freeze-dried for 48 h. After weighing, the dried anemones were combusted for 12 h at 500°C and the ash-free dry weight (AFDW) was obtained by subtracting ash weight from dry weight.

Analysis of feeding experiments

The natural logarithm of prey concentration was plotted with time, and the expected relationship

$$\ln(C_t) = -Ft + \ln C_0 \quad (1)$$

was fitted to the data using linear regression analysis and tested using Pearson's product-moment correlation (Sokal and Rohlf, 1981). The relationship is a linearization of the function

$$C_t = C_0 e^{-Ft} \quad (2)$$

describing the exponential decrease in prey concentration with time in a closed system (Leversee, 1976) where C_t and C_0 are the concentrations of prey (nauplii l^{-1}) at the times t and t_0 , respectively, and F is the clearance rate (min^{-1}) of the suspension feeder. F depends on the features of the feeding structures such as the size and density of tentacles per square centimeter of tentacle-crown area (Sebens, 1981), orientation relative to flow (Leversee, 1976; Johnson and Sebens, 1993), height above the substratum (Muschenheim, 1987), and prey availability. The total clearance rate of the group of anemones (F_{tot}) was the slope of the regression line $\pm 95\%$ CL, and the maximum feeding rate was determined as $F_{\text{tot}} C_0 V$ (nauplii min^{-1}), where V is the water volume (l) of the system. To account for settlement and accumulation of prey that could not be explained by anemone feeding, control experiments were conducted using anemone mimics. To be able to compare the retention of prey among anemone size classes in a given flow regime, feeding rates were expressed based on ash-free dry weight (AFDW) and square centimeter of tentacle-crown area (S) at t_0 . The empirical, maximum feeding rate per square centimeter of tentacle-crown area was thus determined as

$$\text{Feeding rate}_{\text{Max,cm}^{-2}} = \frac{C_0 V (F_{\text{tot}} - F_{\text{control}})}{S} \quad (3)$$

and the maximum feeding rate per gram of ash-free dry weight was calculated as

$$\text{Feeding rate}_{\text{Max,AFDW}^{-1}} = \frac{C_0 V (F_{\text{tot}} - F_{\text{control}})}{\text{AFDW}} \quad (4)$$

Only the control experiment run at the lowest flow velocity (4 cm s^{-1}) produced a significant depletion rate ($F_{\text{control}} C_0 V \pm \text{CL}$ (nauplii min^{-1}) = 0.36 ± 0.18 , $P = 0.02$), and this was accordingly subtracted from feeding

experiments run at this flow speed. Feeding rates of different size classes at a given flow regime were compared using an unplanned comparison (the Tukey-Kramer method; Sokal and Rohlf, 1981).

Feeding efficiencies (E) are useful in comparing feeding performance among size classes as well as in comparing feeding performance of a size class among flow regimes, and were calculated as the number of prey items captured relative to the number that would pass through the space occupied by the feeding appendages if the latter were not there (see Patterson, 1991). The maximum number of prey items passing the projected feeding surface perpendicular to flow ($S_{j,pr}$, cm²) per unit time is a product of the concentration of prey at t_0 (C_0 , nauplii l⁻¹) and the flow velocity (U_j , cm s⁻¹) at the level of the feeding structures (y), hence

$$N_{\text{passing}} = S_{j,pr} C_0 U_j \frac{1}{1000 \text{ cm}^3} \times \frac{60 \text{ s}}{\text{min}} \quad (5)$$

$S_{j,pr}$ was calculated as an ellipsoid described by the height and width ranges of the tentacle crown (perpendicular to the flow direction), from which the projected, transverse sectional area of the uppermost part of the column (the parapet; see Manuel, 1988) was subtracted. The feeding efficiency (E) was then expressed as

$$E = \frac{N_{\text{captured}}}{N_{\text{passing}}} = \frac{FV}{S_{j,pr} U_j} 16.7 \frac{\text{cm}^3 \text{ l}^{-1}}{\text{s min}^{-1}} \quad (6)$$

where $N_{\text{captured}} = C_0 V F$ (nauplii min⁻¹).

Effect of upstream neighbors

To determine the effect of upstream neighbors on the feeding rate per square centimeter of tentacle crown area, a series of experiments analogous to the above were conducted using six patch sizes of anemones. Patch size was expressed as the number of parallel rows of anemones aligned perpendicular to flow on the bottom of the flume. To exclude variation caused by flow and anemone size, all experiments were conducted using anemones within an intermediate size range (3–4-cm pdd), and run at the flow speed at which this size class had its maximum feeding efficiency (see Results). Effect of upstream neighbors on prey capture per square centimeter of tentacle crown was tested using the Tukey-Kramer method (Sokal and Rohlf, 1981).

Results

Vertical feeding zone and tentacle-crown deformation

The height of tentacle crowns above the flume floor (y , from lowermost to uppermost tentacle tips), and thus vertical feeding zone, of large anemones was 2–3 times that of medium and small anemones, and showed a con-

sistent decline with increasing flow regime (Fig. 2). The feeding zone of large anemones was especially affected by flow—their mean height at the highest flow ($y_{\text{Mean}} \pm \text{SE} = 4.2 \pm 0.2 \text{ cm}$) was only 50% of that recorded at the lowest flow regime ($y_{\text{Mean}} \pm \text{SE} = 8.2 \pm 0.9 \text{ cm}$). A pronounced downstream bending of anemone columns with increasing flow occurred (Fig. 2). The three size classes experienced different local flow velocities (U_j , estimated from flow profiles in Fig. 1) in a given flow regime because of their different positions in the boundary layer. The uppermost tentacles of large anemones experienced about twice the flow velocity of medium and small anemones, which were positioned deeper in the turbulent boundary layer (Figs. 1 and 2). Differences in local flow speeds were less noticeable among medium and small anemones.

Tentacle-crown deformation, indicated by a decreasing ratio of projected tentacle-crown area to ash-free dry weight (S/AFDW) with increasing flow, was most pronounced for large anemones (Table 1). The projected prey-capture surface of large anemones at $U_{10} = 44 \text{ cm s}^{-1}$ was only one-third of that recorded at $U_{10} = 4 \text{ cm s}^{-1}$. Tentacle-crown deformation of small and medium-sized anemones was noticeable only at flows between 4 and 17 cm s⁻¹. In that range they showed an initial increase in S/AFDW , presumably indicating incomplete tentacle-crown extension at the lowest flow velocity. Moreover, the generally lower S/AFDW ratios of large relative to small anemones corroborates earlier findings (Sebens, 1981) that larger *M. senile* have a smaller prey-capture surface per unit of biomass.

Feeding rates

Feeding rates of the three size classes of *M. senile* showed drastic changes with increasing flow, regardless of unit (per polyp, square centimeter of tentacle-crown area, or gram of ash-free dry weight, Fig. 3). Feeding rates tended to increase linearly and monotonically with flow over the range 4–17 cm s⁻¹ for all size classes, indicating that the availability of prey is a function of flow in low to moderate flow regimes. On a per-polyp basis, large anemones captured 3–10 times more nauplii than small and medium-sized anemones within the flow range 4–17 cm s⁻¹ (Fig. 3A). Above 20 cm s⁻¹, however, the feeding rate of large anemones declined rapidly with flow and converged with those of small and medium anemones, which remained constant above 20 cm s⁻¹. On a per-biomass basis, the pattern was partly reversed: small anemones showed 2–3 times higher feeding rates than medium-sized anemones, which in turn showed higher feeding rates than large anemones, over the flow range 10–44 cm s⁻¹ (Fig. 3B). At the slowest flow, medium-sized anemones showed significantly lower feeding rates

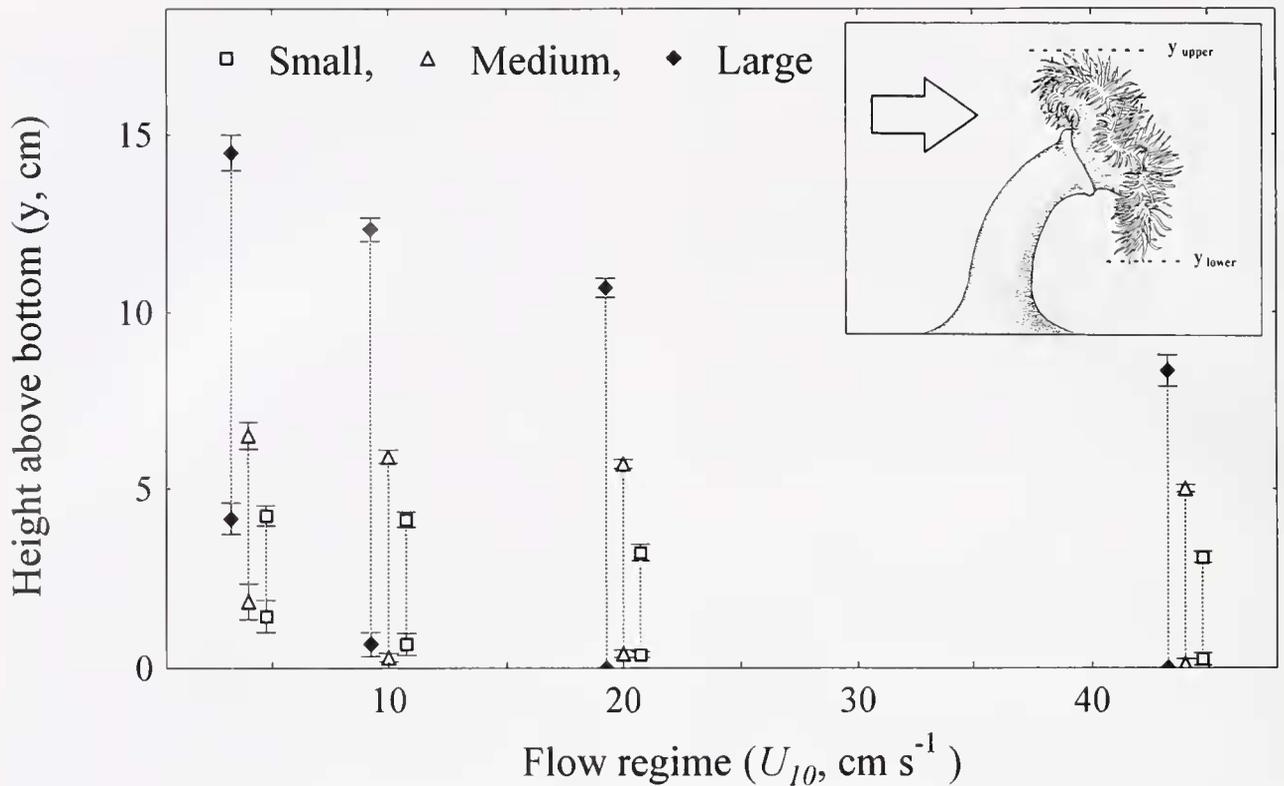


Figure 2. Vertical feeding zone (range of tentacle-crown heights) of the three size classes of *Metridium senile* as a function of flow regime. Error bars are ± 1 SE of 3 to 9 anemones. The inset shows the typical posture of a medium-sized anemone at moderate flow; the arrow indicates flow direction. Small anemones: 1.0–2.0 cm in pedal disc diameter (pdd), medium: 2.5–3.0 cm pdd, and large: 6.0–6.5 cm pdd.

than did both small and large anemones. Interestingly, feeding rates based on feeding-surface area (S , Fig. 3C) and on anemone biomass displayed the same general patterns, perhaps reflecting isometric growth (Sebens, 1981). One noticeable difference among the sets of data is, however, that large anemones showed a significant de-

crease in prey capture per unit biomass at $U_{10} > 17 \text{ cm s}^{-1}$.

Feeding efficiencies

The three size classes of *M. senile* demonstrated three distinct flow optima, inversely related to size class, at

Table 1

Flow-induced tentacle-crown deformation and anemone biomass in three size classes of *Metridium senile*

U_{10} (cm s^{-1})	n	Small (1.0–2.0 cm pdd)		n	Medium (2.5–3.0 cm pdd)		n	Large (5.5–6.0 cm pdd)	
		$S/\text{AFDW} \pm$ SE ($\text{cm}^2 \text{g}^{-1}$)	$\text{AFDW} \pm$ SE (g)		$S/\text{AFDW} \pm$ SE ($\text{cm}^2 \text{g}^{-1}$)	$\text{AFDW} \pm$ SE (g)		$S/\text{AFDW} \pm$ SE ($\text{cm}^2 \text{g}^{-1}$)	$\text{AFDW}^* \pm$ SE (g)
4	9	64.99 ± 6.24	0.156 ± 0.019	7	43.86 ± 2.44	0.635 ± 0.048	3	56.31 ± 7.14	2.827 ± 0.403
10	6	84.09 ± 3.18	0.148 ± 0.009	5	49.52 ± 3.31	0.682 ± 0.052	3	53.67 ± 7.48	2.827 ± 0.403
17	8	52.48 ± 3.99	0.159 ± 0.022	5	40.86 ± 3.31	0.663 ± 0.058	3	43.39 ± 3.92	2.827 ± 0.403
20	8	47.80 ± 2.83	0.160 ± 0.020	5	36.48 ± 1.92	0.650 ± 0.061	3	29.61 ± 3.17	2.827 ± 0.403
28	7	47.80 ± 3.61	0.101 ± 0.015	—	—	—	—	—	—
44	6	44.74 ± 3.96	0.148 ± 0.009	4	36.37 ± 1.09	0.541 ± 0.016	3	20.56 ± 4.16	2.827 ± 0.403

Size classes were based on measurement of pedal disc diameter (pdd). The degree of tentacle-crown deformation is quantified as the decrease in ratio of tentacle crown area (S) to ash-free dry weight (AFDW) with increasing flow (U_{10}). SE denotes standard error of $n = 3$ to 9 anemones.

* The same three large anemones were exposed to all flow regimes.

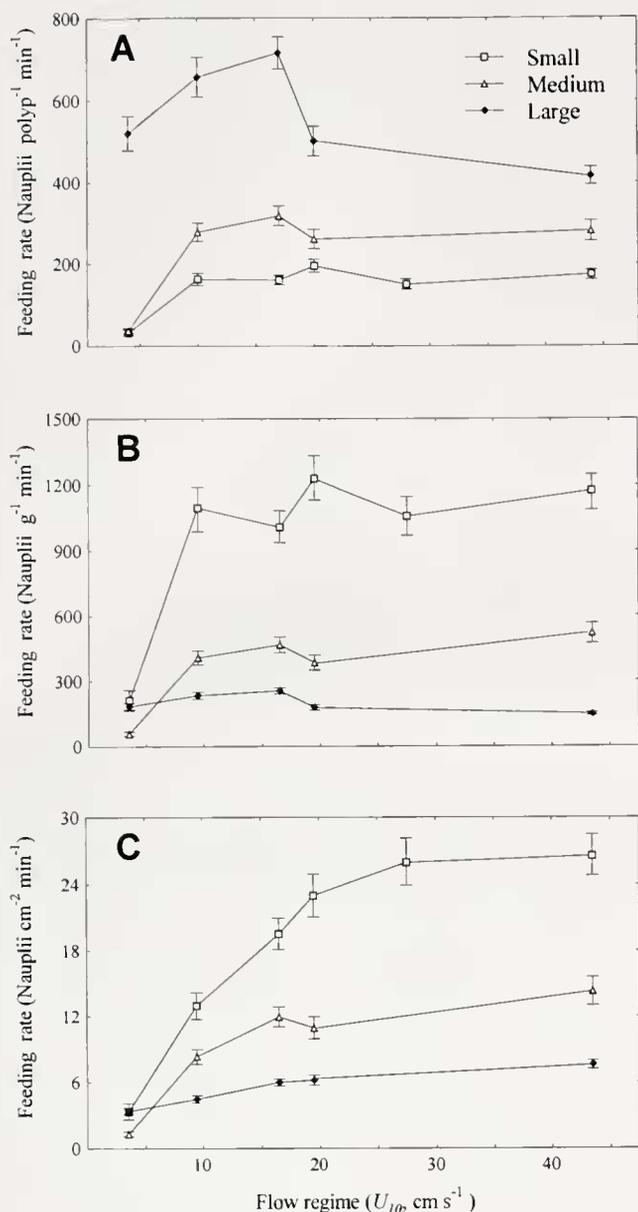


Figure 3. Feeding rates (nauplii min⁻¹) per (A) polyp, (B) gram of ash-free dry weight, and (C) unit area of tentacle crown of *Metridium senile* as a function of body size and flow regime. Error bars are $\pm 95\%$ confidence limits. All comparisons among size classes are significant at any given flow regime except at $U_{10} = 4$ cm s⁻¹. Groups with overlapping error bars are not significantly different by the Tukey-Kramer test. Regressions for the determination of F were highly significant in all experiments ($P < 0.001$, $R > 0.88$).

which the feeding efficiency (E) was maximized (Fig. 4). Large anemones showed a maximum feeding efficiency at the slowest flow ($U_{10} = 4$ cm s⁻¹), medium-sized anemones at low to moderate flows (10–17 cm s⁻¹), and small anemones at moderate to high flows (10–20 cm s⁻¹). Small anemones were able to capture and re-

tain up to $25.7 \pm 2.0\%$ of the nauplii passing the projected area of the tentacle crown at their optimal flow speed ($U_{10} = 20$ cm s⁻¹). The feeding efficiency of all size classes decreased monotonically beyond their optimum. At all flow velocities except the lowest one, small anemones were significantly (2–3 times) more efficient than medium-sized anemones, which in turn were about twice as efficient as large anemones; these results are analogous to the pattern of feeding rates based on biomass and area of feeding surface.

Effect of upstream neighbors

The feeding rate per unit area of tentacle crown of medium-sized *M. senile* declined significantly with increasing numbers of conspecifics upstream (6.45 ± 0.45 to 2.25 ± 0.30 nauplii min⁻¹ cm⁻², both $\pm 95\%$ CL) (Fig. 5). The effect of upstream neighbors was most pronounced within small aggregations of anemones (2–4 rows). Increasing the number of aligned rows of anemones from 7 to 16 did not reduce the feeding rate per unit area of tentacle crown, and thus indicated a threshold at which the feeding rate per polyp was unaffected by the addition of upstream neighbors.

Discussion

Feeding rates and efficiencies

The combinations of polyp size and flow regime at which prey capture of *Metridium senile* is maximized are in good agreement with the pattern of population structures and flow habitats observed in the field, suggesting that size distributions of *M. senile* are, in part, based on the ability to utilize seston flux. Interestingly, small anemones were generally more efficient at retaining prey than both medium and large anemones over the full flow range. Large anemones were, however, more than twice as efficient as medium-sized anemones at the slowest flow, but this relationship was reversed at moderate to high flow. The generally higher feeding rate per unit area and per unit biomass of small anemones may allow rapid growth to a size at which they can better compete for space, avoid size-selective predation (Harris, 1986), and reproduce sexually (Anthony and Svane, 1994), provided that the energy input is used in polyp growth rather than in clonal growth by pedal laceration (see below). The maximized feeding at a high flow speed of small *M. senile* is inconsistent with other studies on prey capture (e.g., Okamura, 1984, 1985; McFadden, 1986; Best, 1988; Leonard *et al.*, 1988; Dai and Lin, 1993) and growth (Okamura, 1992; Eckman and Duggins, 1993) of tentaculate suspension feeders. In these studies maximum rates of feeding, growth, or both were generally associated with low flow speeds. A direct comparison

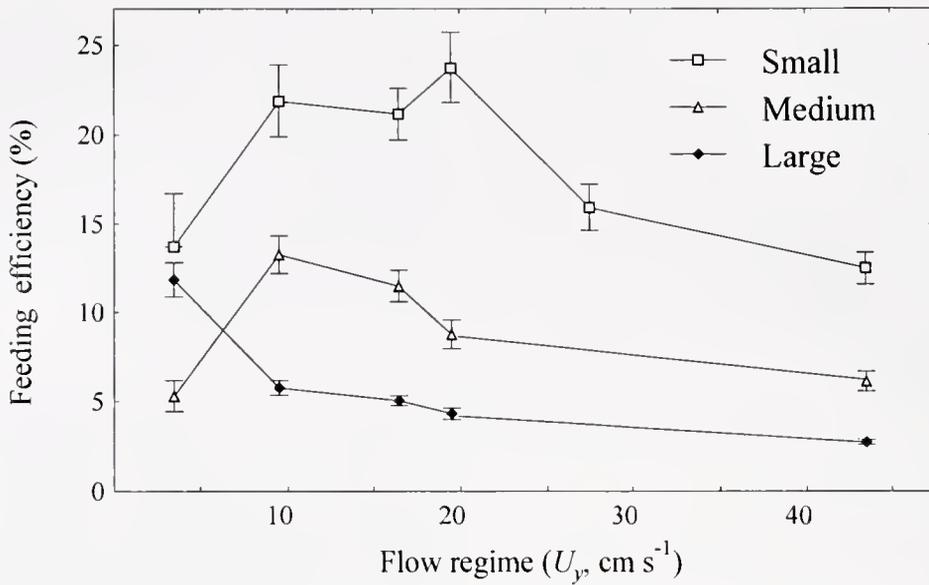


Figure 4. Feeding efficiency (number of nauplii captured per number of nauplii passing, see Eq. 5 and 6) as a function of flow regime in three size classes of *Metridium senile*. Error bars are $\pm 95\%$ confidence limits. All comparisons among size classes are significant at any given flow regime except between small and large anemones at $U_{10} = 4 \text{ cm s}^{-1}$. Groups with overlapping error bars are not significantly different by the Tukey-Kramer test.

among studies of flow, body size, and prey capture is difficult, however, because different ranges of size and flow regime are used in different studies. Also, compari-

sons of size *per se* among different taxa of suspension feeders are complicated by differences in their structural organization.

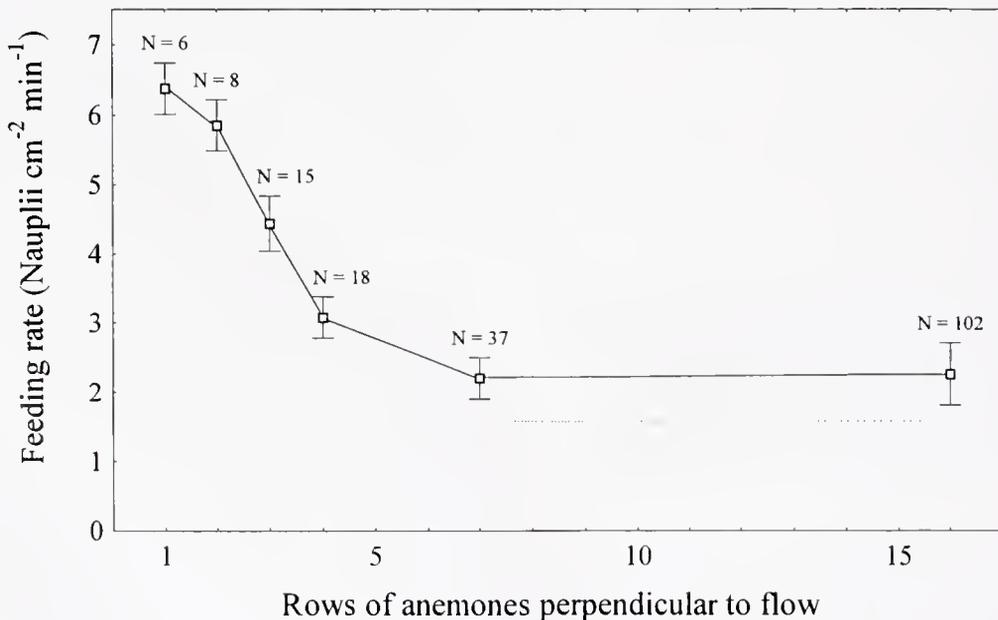


Figure 5. Effects of upstream neighbors in *Metridium senile*. Feeding rate (nauplii min^{-1}) per square centimeter of tentacle crown as a function of the number of upstream conspecifics. Error bars are $\pm 95\%$ confidence limits. Groups underlined at the same level are not significantly different by the Tukey-Kramer test.

The maximum prey-capture efficiency of *M. senile* from the Gullmarsfjord ($25.6 \pm 2.0\%$, small anemones) is only half of that reported by Lesser *et al.* (1994) for *M. senile* from the Gulf of Maine (40% for offshore and 52% for coastal anemones). Data on prey capture were, however, not given in relation to flow speed although a significant tentacle-crown deformation (50%) at increasing flow was recorded, as also found in this study. The feeding efficiencies determined for *M. senile* in this study are also generally lower than those of the sea pen *Ptilosarcus gurneyi* (Best, 1988) which were up to 42%, decreasing with flow to 30% within a narrow low-flow range (1.5–5.0 cm s⁻¹), but are comparable with whole-colony efficiencies of the octocoral *Alcyonium siderium* (Patterson, 1991) in moderate flow regimes. However, the feeding efficiency of *A. siderium* is inversely related to both colony size and flow speed (Patterson, 1991), whereas the relationship between feeding, size, and flow shows a more complex pattern in *M. senile*. These different patterns may, in part, be due to the different filtering structures and tentacular organizations between solitary and colonial anthozoans, and to differences in structural flexibility.

The increasing feeding rates as a function of ambient flow within the low to moderate flow range corroborates earlier assumptions that moderate-flow habitats provide higher seston availability than low-flow habitats (Shick and Hoffmann, 1980; Sebens, 1984; Shick, 1991). The flow range at which food intake per polyp or per biomass is maximized, however, is different between size classes. Large anemones showed a relatively distinct maximum at 10–17 cm s⁻¹, whereas small and medium anemones maintained a constant food intake above 10 cm s⁻¹. These different responses to flow are likely to explain, in part, the differences in size distribution of *M. senile* across flow habitats. In high-flow habitats *M. senile* typically forms dense aggregations of small anemones monopolizing vast areas of rock wall and consisting of only a few clones, whereas populations in low-flow habitats often comprise large and usually more scattered individuals from numerous clones (Anthony and Svane, 1994).

Only at the slowest flow were large anemones able to achieve feeding rates and feeding efficiencies comparable to those of small and medium-sized anemones. Large anemones had a significant feeding disadvantage relative to small and medium anemones at flows greater than 10 cm s⁻¹, and displayed a per-biomass food intake only one-eighth that of the small anemones in very high flow regimes. One explanation for this pattern is based on differences in the geometry of the tentacle crown of large and small anemones. Although the tentacles of large and small *M. senile* have comparable geometry and size (Sebens, 1981), the relative size of the oral disc increases with body size. Therefore, the proportion of tentacle crown

effective in upstream capture (the circumference of tentacles facing upstream or perpendicular to flow) when the anemone is bent downstream relative to the total tentacle crown area is likely to be greater for small anemones. Subtracting the projected area of the upper part of the column from the surface area of the tentacle crown accounted to some extent for such geometric differences. However, size-related differences in the spacing of openings in the capitulum at the base of the tentacles were not accounted for. If such differences exist, mainly as a result of differential convolutions of the tentacle crown, they are likely to affect the size-specific feeding efficiencies (J. M. Shick, pers. com.).

In moderate to high flow velocities, a great proportion of the tentacle crown of large anemones is hidden from the upstream flux and is thus engaged in wake feeding, which is likely to be less effective than upstream feeding (Shimeta and Jumars, 1991). Small anemones may benefit from both upstream and wake feeding at comparable flow rates, whereas wake feeding is likely to be the predominant mode of feeding for large anemones in moderate to high flow. However, due to the higher Reynolds number associated with large animals (Shimeta and Jumars, 1991), downstream vortex formation is more pronounced for large anemones. This effect may, in part, be beneficial in providing a leeward region of enhanced retention efficiency through reduced flow velocities (Patterson, 1984).

Although the probability of prey encounter increases with flow, so does the risk of dislodgement of captured prey, and an optimum local velocity must be within the range over which retention significantly exceeds dislodgement of encountered prey. Both the capacity for retention by and the risk of dislodgement from the tentacles of sea anemones and of passive suspension feeders in general may vary among size classes and among genotypes. The small *M. senile* from high-flow habitats may be better adapted to feeding in a high-flow environment by being equipped with a more efficient cnidom for both subduing and retaining intercepted prey. Effects of flow forces on dislodgement of intercepted prey in cnidarian suspension feeders are, however, poorly understood (Patterson, 1984; Shimeta and Jumars, 1991).

Vertical feeding zone and tentacle-crown deformation

The prey availability can for some passive suspension feeders be adjusted to a given flow regime by means of behavior or change of posture, for example by regulating the height and orientation of the feeding appendages (ophiuroids: Warner and Woodley (1975); crinoids: Holland *et al.* (1987), Leonard (1989); sea anemones: Robbins and Shick (1980), this study; polychaetes: Muschenheim (1987), Shimeta and Jumars, (1991)) or by vertical,

oriented locomotion of the whole animal (Anthony and Svane, 1995). Differences in prey capture among small, medium, and large *M. senile* in this study could not be explained fully by different local flow velocities at different heights in the boundary layer. In fact, the local flow velocities experienced at the mean level of the tentacle crown of the three size classes in low to moderate flow regimes did not differ by more than 1–2 cm s⁻¹. Contrasting local flow velocities due to differences in vertical position were found only between large and small or medium-sized anemones at the highest flow regime (6–8 cm s⁻¹). A higher degree of downstream bending of medium-sized and especially large anemones due to proportionately greater drag (Koehl, 1977a) explains the overlapping, vertical feeding zones of different size classes. Flow forces thus act in moving the feeding apparatus of large anemones into the boundary layer and away from the maximum exposure, enabling some, though reduced, prey capture at even the highest ambient flow.

Tentacle-crown deformation, and thereby a reduced prey-capture area normal to flow, could to some extent account for the significantly lower feeding success of large anemones in regimes of moderate to high flow. Prey-capture surface per unit biomass decreased by more than 50% when altering the flow regime from 4 to 44 cm s⁻¹, affecting the volume of water filtered and the rate of potential prey encounter accordingly, and probably also the spacing between tentacles (see also Lesser *et al.*, 1994). Best (1988) also found that the deformability of the sea pen *Ptilosarcus gurneyi* strongly affected filtration efficiency and volume of water filtered. The effectiveness of the feeding apparatus of a large, soft-bodied suspension feeder is intrinsically apt to be more constrained by flow forces than is that of a small suspension feeder, because large animals are subject to proportionately greater drag (Koehl, 1977a) and shear stresses (Koehl, 1977b) than are small animals in similar flow conditions. Since the potential prey capture of, for example, a sea anemone is a function of the surface area of the feeding apparatus (Sebens, 1981), the *S*/AFDW ratio is likely to be a useful indicator of flow-habitat suitability.

Feeding rates vs. metabolic cost

To determine flow optima of passive suspension feeders, information on both energy intake and metabolic cost is necessary for every flow regime (Sebens, 1979, 1982). Although the pattern of feeding rates per unit of biomass suggests that small anemones generally have a greater energy surplus than large and medium-sized anemones regardless of flow regime, energy demand is likely to vary among size classes as well as among flow regimes. Gas exchange, and thus metabolic cost, in cnid-

arians is largely governed by the thickness and characteristics of the boundary layer surrounding the organism, which in turn are functions of organism size and flow regime (Patterson, 1992a). For example, Patterson and Sebens (1989) found that the rate of respiration in large specimens of *Metridium* doubled over the flow range 7–15 cm s⁻¹ due to the effect of water motion. A useful method for comparing metabolic cost across flow regimes as well as size classes is the relationship between Sherwood number and Reynolds number (Patterson and Sebens, 1989; Patterson, 1992a, b). Sherwood number (*Sh*) is a dimensionless index of metabolism, defined as the ratio of mass flux per unit surface area assisted by convection (F_{conv} , $\mu\text{ cm}^{-2}\text{ h}^{-1}$) to that which would occur if diffusion through a stagnant layer of water was the only mechanism of gas exchange. Reynolds number (*Re*) is the ratio of inertial to viscous forces acting on the flowing water, and is an index of the strength of flow experienced by the organism. For *Metridium*, the functional relationship between *Sh* and *Re* is $Sh = 0.28 Re^{1.04}$ as found by Patterson and Sebens (1989). Since *Re* is a function of body size and flow [$Re = U_y \times \text{TCD}/\nu$, where U_y is local flow speed (cm s⁻¹), TCD is tentacle-crown diameter (cm), and ν is the kinematic viscosity of seawater ($1.04 \times 10^{-2}\text{ cm}^2\text{ s}^{-1}$)], *Sh* can be readily obtained for all combinations of flow regime and size class in this study. Expected (flow-assisted) metabolic cost can be derived from *Sh* as the convective mass flux (F_{conv} , the numerator of *Sh*), normalized to biomass by multiplying with the ratio of surface area to biomass (*SA*/AFDW, $\text{cm}^2\text{ g}^{-1}$), where *SA* is the sum of tentacle surface area [see regressions in Sebens (1981)] and surface area of the column. According to Patterson (1992b) convective mass flux can be calculated as $F_{\text{conv}} = Sh \times D(C_e - C_i)/\text{TCD}$, where *D* is the diffusion coefficient for oxygen ($7.2 \times 10^{-2}\text{ cm}^2\text{ h}^{-1}$), C_e is the oxygen concentration in the surrounding water ($\approx 7\text{ mg l}^{-1}$), and C_i is the oxygen concentration at the site of metabolism. For azooxanthellate cnidarians, C_i can be regarded as negligible (pers. com., Mark Patterson). Expected metabolic rate per unit biomass ($R_{\text{exp}} = Sh \times D \times C_e \times SA/[\text{TCD} \times \text{AFDW}]$, $\mu\text{g (g dry wt)}^{-1}\text{ h}^{-1}$) as a function of flow regime for the three size classes of *M. senile* is shown in Figure 6.

Expected metabolic rate for all size classes increases as a linear function of flow regime, with a 10-fold increase in metabolic rate between lowest and highest flow speeds. In accordance with allometric studies (*e.g.*, Sebens, 1981), metabolic rate is greater for small and medium-sized compared to large anemones, by a factor of about $\frac{3}{2}$. Interestingly, expected metabolic rate is higher for medium-sized compared to small anemones at flow regimes greater than 10 cm s⁻¹, probably due to the higher local flow speeds (and hence *Sh*) experienced by medium-sized anemones (Figs. 1 and 2). Although energy

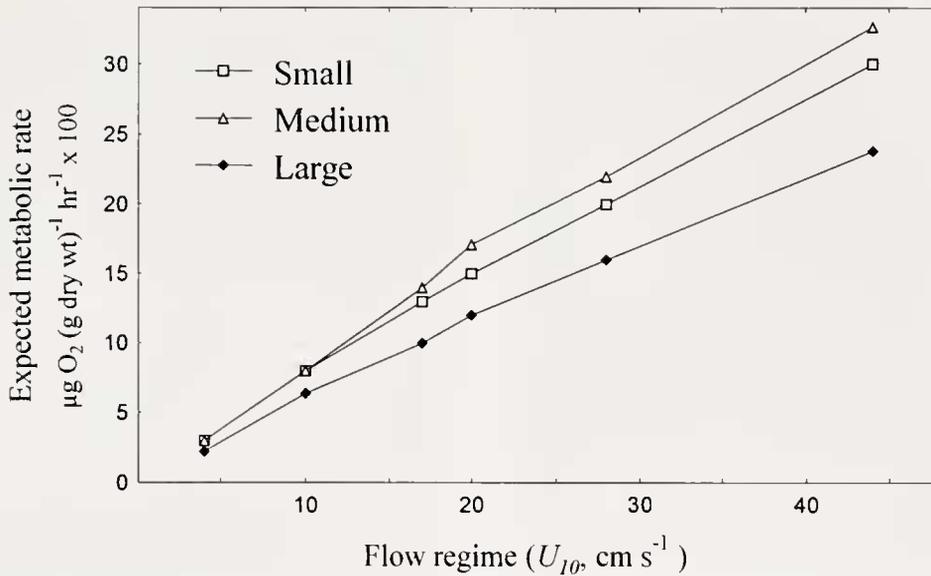


Figure 6. Expected metabolic rate as a function of flow regime for the three size classes of *Metridium senile*, based on mean Reynolds numbers for the study anemones and empirical mass-transfer relations from Patterson and Sebens (1989). See text for calculations.

balance also depends on local food availability, food quality, and absorption efficiency (e.g., Zamer, 1986), the patterns of potential food intake (feeding rate) and expected metabolic cost provide a basis for relative comparisons of potential flow optima among size classes. The flow speed at which energetic cost counterbalances food intake will be highest for the small anemones, intermediate for medium-sized anemones, and lowest for large anemones. Due to very high feeding rates, small anemones are able to maintain a more positive energy balance than both medium and large anemones at all flow speeds $\geq 10 \text{ cm s}^{-1}$. The almost 10-fold increase in feeding rate of small anemones in the flow range $4\text{--}10 \text{ cm s}^{-1}$ amply exceeds the concomitant increase in metabolic cost over this flow interval, and is likely to allow rapid growth of juvenile anemones and lacerates in low-to-moderate flow regimes. At higher flow speeds, however, feeding rate remains constant, whereas metabolic rate increases linearly with flow. If the feeding rate of small anemones at 4 cm s^{-1} is sufficient to meet basic energy demands, so is the feeding rate at 44 cm s^{-1} because both feeding rate and metabolic cost increase 10-fold between lowest and highest flow. At the lowest flow speed, however, large anemones are likely to have a more positive energy balance than the smaller size classes, given the comparable feeding rates of small and large anemones but the lower mass-specific metabolic cost of large anemones. Since large anemones only showed low weight-specific feeding rates without a convincing maximum, any energetic optimum of this size class must be confined to low-flow regimes because of the rapid increase in metabolic rate

with flow. The flow optimum of medium-sized anemones, on the other hand, is likely to be located in the range $10\text{--}20 \text{ cm s}^{-1}$, as their feeding rate is minimal at 4 cm s^{-1} ($1/3$ of large and small anemones) and their expected metabolic cost increases with flow at a relatively higher rate than for the two other size classes.

Use of mass-transfer theory to compare metabolic cost between individual *M. senile* in different flow regimes does not, however, take into account the differences in spatial distributions between large and small anemones. Large anemones are often widely separated from one another, whereas small anemones (due to their pronounced clonality) form dense patches structurally resembling coral colonies (Anthony and Svane, 1994). Flow around individual polyps in such patches is likely to be further reduced, resulting in a thicker diffusive boundary layer and a lower gas exchange than for small, spatially isolated individuals in similar flow habitats (see also Patterson and Sebens, 1989).

Effects of flow and feeding on reproductive patterns

One way in which *M. senile* might maintain an energetically optimal polyp size in the prevailing current regime is by altering the rate of pedal laceration. Laceration is a loss of tissue to the individual polyp (facilitating degrowth), but also an effective means of clonal growth, so differential rates of laceration between local populations may have consequences for their size distributions. The generally higher rates of laceration in populations of small *M. senile* from high-flow habitats relative to popu-

lations of large anemones from low-flow habitats support this hypothesis (Shick and Hoffmann, 1980; Anthony and Svane, 1994). Since large anemones cannot maintain a positive energy balance in high-flow habitats, whereas small anemones can, any excess energy acquired by high-flow anemones is likely to be allocated to clonal growth (through pedal laceration) rather than to polyp growth. Laceration is also stimulated by feeding (Bucklin, 1987), suggesting that asexual reproduction is one pathway by which energy surplus is translated into a greater genet biomass. Effects of feeding and ambient flow on laceration are, however, apt to be closely linked due to the direct proportionality between flow and seston flux, and hence potential particle encounter. By obtaining an optimal polyp size in a given flow habitat through growth or degrowth (*via* laceration), the energy available for clonal growth, sexual reproduction, and hence genet fitness can be further enhanced. Clonal growth as opposed to polyp growth in high-flow habitats creates the energetic potential for the genet to grow indefinitely without size-energy constraints, because the addition of new polyps to the clone increases feeding surface and energetic cost linearly (Sebens, 1979). Conversely, growth to a maximum polyp size in low-flow habitats enables maximum feeding and thus energy input (this study), and also a maximum per-biomass reproductive output (Anthony and Svane, 1994).

Effect of upstream neighbors

Considering the clonal nature and high polyp densities of most populations of *M. senile*, the presence of upstream neighbors is likely to be an important factor affecting the energy input of both the polyp and the clone. Furthermore, the effect of upstream neighbors on near-bed prey availability downstream may select for large size in some flow habitats, despite a relatively greater food intake in small anemones, and thereby contribute to structuring local populations. The asymptotic relationship between feeding rate per unit area of tentacle crown and number of upstream conspecifics, on the other hand, indicated that the potential feeding capacity was not reduced to below about 30% of the situation without neighbors upstream. A likely explanation for this threshold is that individual anemones function as roughness elements, increasing turbulence and eddy diffusivity downstream (Denny, 1988), thereby reducing local particle depletion around tentacle crowns by mixing mainstream water into the turbulent boundary layer. In high-flow habitats, the generally higher density of anemones may also provide shelter for individual anemones by moving the turbulent boundary layer outward. As suggested by Patterson (1984), particle lift in the boundary layer over the tentacle-crown canopy may be

responsible for reduced downstream concentrations, and thereby, in part, account for the asymptotic rather than linear reduction in retention with increasing number of upstream neighbors (see also Fr  chette *et al.*, 1989). Furthermore, gravitational deposition is likely to be more important in dense clones than in populations of scattered individuals on horizontal substrata, providing a "rain" of seston that is independent of the number of upstream neighbors. Overall, these results suggest that increased clonal growth of *M. senile* in high-flow habitats at the expense of polyp growth (see review by Shick, 1991) may negatively affect net prey capture by the genet through feeding interaction between clonemates. Conversely, predominant polyp growth and reduced clonal growth in low-flow habitats is likely to enhance prey capture by excluding the effect of neighbors. The generally higher feeding efficiency of small polyps of *M. senile* may, however, compensate for the negative effects of neighbors in dense, clonal aggregations if the prevailing flow conditions provide a correspondingly higher flux of prey.

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Literature Cited

- Anthony, K. R. N., and I. Svane. 1994. Effects of flow-habitat on body size and reproductive patterns in the sea anemone *Metridium senile* (L.) in the Gullmarsfjord, Sweden. *Mar. Ecol. Prog. Ser.* **113**: 257-269.
- Anthony, K. R. N., and I. Svane. 1995. Effects of substratum instability on locomotion and pedal laceration in *Metridium senile* L. (Anthozoa: Actiniaria). *Mar. Ecol. Prog. Ser.* **124**: 171-180.
- Best, B. A. 1988. Passive suspension feeding in a sea pen: effects of ambient flow on volume flow rate and filtering efficiency. *Biol. Bull.* **175**: 332-342.
- Bucklin, A. 1987. Growth and asexual reproduction of the sea anemone *Metridium*: comparative laboratory studies of three species. *J. Exp. Mar. Biol. Ecol.* **110**: 41-52.

- Dai, C.-F., and M.-C. Lin. 1993. The effects of flow on feeding of three gorgonians from southern Taiwan. *J. Exp. Mar. Biol. Ecol.* **173**: 57-69.
- Denny, M. 1988. *Biology and the mechanisms of the wave-swept environment*. Princeton University Press, Princeton.
- Eckman, J. E., and D. O. Duggins. 1993. Effects of flow speed on growth of benthic suspension feeders. *Biol. Bull.* **185**: 28-41.
- Fautin, D. G., A. Bucklin, and C. Hand. 1989. Systematics of the sea anemones belonging to genus *Metridium* (Coelenterata: Actinaria), with a description of *M. giganteum* new species. *Wasmann J. Biol.* **47**(1-2): 77-85.
- Francis, L. 1979. Contrasts between solitary and clonal lifestyles in the sea anemone *Anthopleura elegantissima*. *Am. Zool.* **19**: 669-681.
- Fréchet, M., C. A. Butman, and W. R. Geyer. 1989. The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder *Mytilus edulis* L. *Limnol. Oceanogr.* **34**: 19-36.
- Harris, L. G. 1986. Size-selective predation in a sea anemone, nudibranch, and fish food chain. *Veliger* **29**: 38-47.
- Hoffmann, R. J. 1976. Genetics and asexual reproduction of the sea anemone *Metridium senile*. *Biol. Bull.* **151**: 478-488.
- Hoffmann, R. J. 1986. Variation in contributions of asexual reproduction to the genetic structure of populations of the sea anemone *Metridium senile*. *Evolution*. **40**(2): 357-365.
- Holland, N. D., A. B. Leonard, and J. R. Strickler. 1987. Upstream and downstream capture during suspension feeding by *Oligometra serripinna* (Echinodermata: Crinoidea) under surge conditions. *Biol. Bull.* **173**: 552-556.
- Johnson, A. S. 1990. Flow around phoronids: consequences of a neighbor to suspension feeders. *Limnol. Oceanogr.* **35**: 1395-1401.
- Johnson, A. S., and K. P. Sebens. 1993. Consequences of a flattened morphology: effects of flow on feeding rates of the scleractinian coral *Meandrina meandrites*. *Mar. Ecol. Prog. Ser.* **99**: 99-114.
- Koehl, M. A. R. 1976. Mechanical design in sea anemones. Pp. 23-31 in *Coelenterate Ecology and Behavior*, G. O. Mackie, ed. Plenum Press, New York.
- Koehl, M. A. R. 1977a. Effects of sea anemones on the flow forces they encounter. *J. Exp. Biol.* **69**: 87-105.
- Koehl, M. A. R. 1977b. Mechanical organization of cantilever-like sessile organisms: sea anemones. *J. Exp. Biol.* **69**: 127-142.
- LaBarbera, M. J., and S. Vogel. 1976. An inexpensive thermistor flowmeter for aquatic biology. *Limnol. Oceanogr.* **21**: 750-756.
- Leonard, A. B. 1989. Functional response in *Antedon mediterranea* (Lamarck) (Echinodermata: Crinoidea): the interaction of prey concentration and current velocity on a passive suspension feeder. *J. Exp. Mar. Biol. Ecol.* **127**: 81-103.
- Leonard, A. B., J. R. Strickler, and N. D. Holland. 1988. Effects of current speed on filtration during suspension feeding in *Oligometra serripinna* (Echinodermata: Crinoidea). *Mar. Biol.* **97**: 111-125.
- Lesser, M. P., J. D. Witman, and K. P. Sebens. 1994. Effects of flow and seston availability on scope for growth of benthic suspension-feeding invertebrates from the Gulf of Maine. *Biol. Bull.* **187**: 319-335.
- Leversee, G. J. 1976. Flow and feeding in the fan-shaped colonies of the gorgonian coral. *Leptogorgia*. *Biol. Bull.* **151**: 344-356.
- Mannell, R. L. 1988. *Synopsis of the British Fauna: New Series 18, British Anthozoa*. Academic Press, London.
- McFadden, C. S. 1986. Colony fission increases particle capture rates of a soft coral: advantages of being a small colony. *J. Exp. Mar. Biol. Ecol.* **103**: 1-20.
- Muschenheim, D. K. 1987. The dynamics of near-bed seston flux and suspension-feeding benthos. *J. Mar. Res.* **45**: 473-496.
- Okamura, B. 1984. The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of Bryozoa. I. *Bugula stolonifera* Ryland, an arborescent species. *J. Exp. Mar. Biol. Ecol.* **83**: 179-193.
- Okamura, B. 1985. The effects of ambient flow velocity, colony size, and upstream colonies on the feeding success of Bryozoa. II. *Conopeum reticulatum* L., an encrusting species. *J. Exp. Mar. Biol. Ecol.* **89**: 69-80.
- Okamura, B. 1992. Microhabitat variation and patterns of colony growth and feeding in a marine bryozoan. *Ecology* **73**(3): 1502-1513.
- Patterson, M. R. 1984. Patterns of whole colony prey capture in the octocoral *Alcyonium siderium*. *Biol. Bull.* **167**: 613-629.
- Patterson, M. R. 1991. Passive suspension feeding by an octocoral in plankton patches: empirical test of a mathematical model. *Biol. Bull.* **180**: 81-92.
- Patterson, M. R. 1992a. A mass transfer explanation of metabolic scaling relations in some aquatic invertebrates and algae. *Science* **255**: 1421-1423.
- Patterson, M. R. 1992b. A chemical engineering view of cnidarian symbioses. *Am. Zool.* **32**: 566-582.
- Patterson, M. R., and K. P. Sebens. 1989. Forced convection modulates gas exchange in cnidarians. *Proc. Natl. Acad. Sci. USA* **86**: 8833-8836.
- Purcell, J. E. 1977. The diet of large and small individuals of the sea anemone *Metridium senile*. *Bull. S. C. Acad. Sci.* **76**: 168-172.
- Robbins, R. E., and J. M. Shick. 1980. Expansion-contraction behavior in the sea anemone *Metridium senile*: environmental cues and energetic consequences. Pp. 101-116 in *Nutrition in the Lower Metazoa*, D. C. Smith and Y. Tiffon, eds. Pergamon Press, Oxford.
- Sebens, K. P. 1979. The energetics of asexual reproduction and colony formation in benthic marine invertebrates. *Am. Zool.* **19**: 683-697.
- Sebens, K. P. 1980. The regulation of asexual reproduction and indeterminate body size of the sea anemone *Anthopleura elegantissima* (Brandt). *Biol. Bull.* **158**: 370-382.
- Sebens, K. P. 1981. The allometry of feeding, energetics, and body size in three sea anemone species. *Biol. Bull.* **161**: 152-171.
- Sebens, K. P. 1982. The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology* **63**(1): 209-222.
- Sebens, K. P. 1984. Water flow and coral colony size: interhabitat comparisons of the octocoral *Alcyonium siderium*. *Proc. Natl. Acad. Sci. USA* **81**: 5473-5477.
- Sebens, K. P., and M. A. R. Koehl. 1984. Predation on zooplankton by the benthic anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actinaria) in the New England subtidal. *Mar. Biol.* **81**: 255-271.
- Shick, J. M. 1991. *A Functional Biology of Sea Anemones*. Chapman & Hall, London.
- Shick, J. M., R. J. Hoffmann, and A. N. Lamb. 1979. Asexual reproduction, population structure, and genotype-environment interactions in sea anemones. *Am. Zool.* **19**: 699-713.
- Shick, J. M., and R. J. Hoffmann. 1980. Effects of the trophic and physical environments on asexual reproduction and body size in the sea anemone *Metridium senile*. Pp. 211-216 in *Developmental and Cellular Biology of Coelenterates*, P. Tardent and R. Tardent, eds. Elsevier/North Holland Biomedical Press, Amsterdam.
- Shick, J. M., and H. B. Dowse. 1985. Genetic basis of physiological variation in natural populations of sea anemones: intra- and interclonal analyses of variance. *Proc. 19th European Marine Biology Symposium*, Cambridge. P. E. Gibbs, ed. Cambridge University Press, UK.
- Shimeta, J., and P. A. Jumars. 1991. Physical mechanisms and rates

- of particle capture by suspension feeders. *Oceanogr. Mar. Biol. Ann. Rev.* **29**: 191-257.
- Sokal, R. R., and F. J. Rohlf. 1981.** *Biometry*. 2 ed. W. H. Freeman & Co. San Francisco.
- Trager, G., Y. Aचितув, and A. Genin. 1994.** Effects of prey escape ability, flow speed, and predator feeding mode on zooplankton capture by barnacles. *Mar. Biol.* **120**: 251-259.
- Vogel, S. 1981.** *Life in Moving Fluids: the Physical Biology of Flow*. Willard Grant Press, Boston, Massachusetts.
- Wainwright, S. A., and M. A. R. Kochl. 1976.** The nature of flow and the reaction of benthic cnidaria to it. Pp. 5-21 in *Coelenterate Ecology and Behavior*, G. O. Mackie, ed. Plenum Press, New York.
- Warner, G. F. and J. D. Woodley. 1975.** Suspension feeding in the brittle star *Ophiotrix fragilis*. *J. Mar. Biol. Assoc. U.K.* **55**: 199-210.
- Zamer, W. E. 1986.** Physiological energetics of the intertidal sea anemone *Anthopleura elegantissima*. I. Prey capture, absorption efficiency and growth. *Mar. Biol.* **92**: 299-314.